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Neoteny and associated terms

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A new terminology is proposed for all cases of developmental variations or anomalies due to *aneuchrony* (acceleration or retardation of development in ontogeny). These anomalies may be merely described in terms of morphological results : the words chosen to designate them (*paedomorphism*, *paedogenesis*) have in common the prefix *paedo-*. The same anomalies may be classified with respect to the type of developmental processes involved in their appearance : if *retardation* is involved, the anomalies belong to the category of *neoteny s.l.*, and if *acceleration* is involved, to that of *neosystelly* ; both terms begin by the prefix *neo-*. Finally, the terms *neoteny s. str.* and *progenesis* are chosen to designate the two different kinds of *paedogenesis*, due respectively to retardation and acceleration of development.

In 1979, two different papers were independently published (DUBOIS, 1979 ; PIERCE & SMITH, 1979) in which was discussed the use of *neoteny* and of associated terms to describe larval reproduction in Amphibians. DUBOIS's (1979) paper, which had been submitted for publication in early January 1978 (before I had read GOULD's 1977 book), suggested a new terminology for these phenomena. On the basis of a very different line of thought, PIERCE & SMITH (1979) also proposed a new terminology, based in part on that of GOULD (1977) but slightly different from it.

The appearance of these two unrelated papers, bearing almost the same title but leading to very different conclusions, was liable to be a cause of further confusion in this already much controversial field. On the other hand it pointed to the existence of a real need for a critical reevaluation of the concepts and terms already in use, and for the establishment of a new and stable terminology. For this reason I submitted on 1st July 1979 to the *Journal of Herpetology*, where PIERCE & SMITH's (1979) paper had been published, a paper presenting a new proposal of terminology for *neoteny* and associated terms, which was taking into account both the remarks of GOULD (1977) and of PIERCE & SMITH (1979), and mine (DUBOIS, 1979). My hope was that this new proposal would be the basis for a long-needed stability in the terminology of phenomena related to acceleration and retardation in development. However, on 6 September 1979, the reviewer David B. WAKE suggested to postpone publication of this paper because this author had a paper in press on the same question (ALBERCH et al., 1979) where the same topic was approached from a different perspective. WAKE suggested that we enter into a private communication in which we attempt to settle differences prior to publishing amything further on this topic, and perhaps present a joint paper. In a letter to me dated 20 September 1979, he repeated this proposal: "I felt that your paper was logical and well argued. I happen to disagree with you, but these are simple matters of orientation and preference. (...) we might even be able to work toward a collaborative study in an attempt (perhaps futile !) to bring some general agreement concerning major issues in this field." On the basis of these comments, I accepted to withdraw my paper from submission to the *Journal of Herpetology*, in the hope to reach an agreement and come to a common proposal with WAKE, to whom

I wrote on 24 September 1979: "It is not exactly clear to me what are your criticisms of my paper, and on what, on the other hand, you do agree in it. I would be glad if you could send me detailed comments on my paper, and possibly suggestions on what could be included in a possible common paper." I got no answer to this letter until WAKE visited me in Paris in September 1980, and on 3 November 1980 he wrote to me: "I have less interest in this matter than do you, and I am afraid that I do not see the need to have a term for the various situations. (...) What Alberch et al. did was simply to lay out a formalism related to the way in which developmental programs are modified in phylogenesis. We did not deal with the problem of how to differentiate the different ecological end points. (...) I just am not convinced that we need a separate terminology for anomalies."

Since, as is clear from the preceding quote, ALBERCH et al.'s (1979) paper does not address the same problems as my own paper, publication of the latter remains relevant. This paper is therefore reproduced below exactly as it was submitted to the *Journal of Herpetology* and as it should logically have appeared in issue *14* (1) (April 1980) of this journal, along with other comments on PIERCE & SMITH's (1979) paper. The viewpoints expressed in this paper and in ALBERCH et al.'s (1979) one are certainly different, but not necessarily incompatible, and a synthesis of both could possibly be proposed in the future: the journal *Alytes* will be opened to any further comment papers on this question.

PRELIMINARY REMARKS

1. The phenomenons which are to be included in the following discussion are all related to *changes in the time of appearance or in the rate of development of features in the ontogeny*. To be allowed to speak of "changes", one must *compare* the new condition to the ancestral one. To say that a "change" has occurred in the times and delays of development is to say, in other words, that the new development is *abnormal* compared to the ancestral one. Before anything, we needs words to designate both an abnormal *and a normal* development (i.e. "normal" in terms of times and delays).

Only one word is available in this respect : *heterochrony* (see GOULD 1977, for a discussion of this term). Indeed, *heterochrony* is only a particular case of a more general group of anomalies in the times and rates of development. It considers only the situation where *some* features show an abnormal rate of development, while others remain normal: therefore the prefix *hetero-*. But there is also the possibility that *all features* show an abnormal rate of development as compared to the ancestors. Such a development, although the name *homochrony* could apply to it, is not "normal". Therefore I suggest to apply the new term *euchrony (eu-* : well ; *khronos* : time) to developments which are normal in their times and rates, as compared with ancestors, and the new term *aneuchrony* to those which are abnormal. According to this view, *heterochrony* is only one kind of *aneuchrony.*

2. One of the reasons for the large confusion of terms in the terminology of *aneuchrony* is that these terms have been used at least in three purposes: to describe abnormal animals, to account for the processes involved in the origin of these variations, and also to carry some information concerning the relations between ontogeny and phylogeny. These are indeed very different functions, and if these different pieces of information are useful, they should be carried by different words. In this connection, I am suggesting below the use of two different classifications of anomalies, one in terms of processes in development and the other one in terms of the phenotypic results of these processes.

3. As far as the *results* are concerned, all kinds of variations or anomalies due to *aneuchrony* should be referred to general categories and be given general names having a pure descriptive value, irrespective of the processes involved in their appearance, and also of the more or less "general" or "regular" (or conversely "accidental" or "teratological") occurrence of these variations and anomalies in the populations, species or higher taxa considered. The terminology proposed should also be applicable to abnormal phenotypes obtained experimentally, and not merely to phenotypes recorded in nature.

To decide that a phenotype is "abnormal" involves a double operation: first it involves a comparison between two organisms or types of organisms, leading to the conclusion that differences do exist between them for a given character; second it involves a decision as to which one of the two organisms may be considered as exhibiting the character in a primitive or plesiomorphous state, and which one in a derived or apomorphous state; this later one may be considered as "abnormal" as compared with the "ancestral norm" showed by the former one. Decisions concerning *aneuchrony* may therefore be taken only if the organisms compared are (or are supposed to be) the closest relatives at a given level. The level chosen may be very different according to the problem studied: it is equally valid to say that a given "teratological" specimen exhibits an abnormal phenotype, due to *aneuchrony*, as compared with its closest relatives, i.e. the other "normal" specimens of the same population, or to say that a given genus shows signs of *aneuchrony* as compared with its closest relative genus. On the other hand, what is "normal" at one level may be "abnormal" at another, and *vice-versa*. It is therefore always important, when dealing with developmental anomalies, to specify whether the phenotype reported upon is abnormal relative to the population, the species, the genus, the family, etc.

4. As has often been emphasized (e.g. DELSOL, 1977 : 121), since each feature or organ may react or evolve independently, the phenomenons of *aneuchrony* must be studied feature by feature. An animal may well exhibit *aneuchrony* for a single character or organ (*heterochrony*), but *aneuchrony* may also affect the whole phenotype of the animal.

An important point in the study of *aneuchrony* is the distinction between the phenomenons related to the "somatic features" and those related to the "reproductive organs" (e.g. GOULD, 1977 : 229). This distinction has been given an important weight by most authors. However, it is an artificial one. All features are, in some cases at least, liable to react independently: this is not only true for the dissociation between these two sets of characters. In particular, some "somatic features" may well exhibit *aneuchrony* while others don't. In the classification suggested below, I will follow the traditional distinction between both kinds of features, but give it less weight than it has often had.

5. As argued by GOULD (1977), any system of study of *heterochrony* (or of *aneuchrony*) must rely upon a criterion of standardization. Although other criteria could be chosen, especially for the study of special problems, the developmental stage of *adulthood* (attainment of sexual maturity) is certainly the only criterion to have enough generality to be the basis of a general system of classification of phenomenons related to *aneuchrony*. The existence of an "adult stage", as opposed to a "juvenile stage" where animals are unable to reproduce, is a very general condition in the whole animal kingdom, while there is no generality in the subdivisions of the "pre-adult" life (embryo, larva, young, with or without metamorphoses) or of the adult life. The stage of metamorphosis, which could be advocated as a good choice in Amphibians, would have no general value and

should therefore be abandoned. Reference should rather be made to the opposition between "juvenile" ("pre-adult") characters (including larval and "young" characters in the Amphibians) and "adult" characters. Therefore, terms like *neoteny* or *paedogenesis* should not be defined in connection with "larval characters", "larval reproduction" and so on (see e.g. PIERCE & SMITH, 1979), but with "juvenile characters", "juvenile reproduction", etc. Such definitions will have more generality, and it should be recalled that the roots *neo-* and *paedo-* refer to the concepts of "young", "child", which are more general than the concept of "larva".

Although "adulthood" is primarily defined as the stage of attainment of sexual maturity in "normal" animals, attainment of this stage may also, at least in many kinds of organisms, be recognized through the use of other criteria, bearing on the somatic features. In animals like most Amphibians however, the only criteria of adulthood other than sexual maturity are often age (and possibly size), which are not very reliable since age (and size) at adulthood may vary according to environmental conditions. In such cases it may be advisable to substitute to the usual criterion (stage of attainment of sexual maturity) a purely *temporal* criterion (age of attainment of sexual maturity). It may thus be argued that an animal whose gonads are not developed at the normal age (and possibly size) of sexual maturity exhibits signs of *heterochrony* in its development, although in the direction reverse to that usually considered. But this criterion should be used carefully, and only in those cases where "normal" condition, *including its "normal" variability,* is well known.

Such indirect criteria may however be important in some cases, since they are the only ones available for recognizing cases of *homochronic aneuchrony*. For example, the giant tadpoles of Anurans, which are sometimes found, may never reach the "stage of adulthood" (neither with respect to the somatic features nor to the reproductive organs), but they nevertheless clearly exhibit retardation in their development (whatever be the cause of this phenomenon) and should therefore be included in the present classification. Similarly, tadpoles fed with thyroxine may metamorphose much earlier than usual: this is clearly a case of experimental acceleration, even though, in this case, neither the adult stage nor age are reached.

6. GOULD (1977) has discussed in detail the eight categories of *heterochrony* recognized by DE BEER (1930). He very persuasively submitted that all cases of *heterochrony* (and I would add of *aneuchrony* in general) may be reduced to two types of processes: acceleration and retardation. However, he failed to clarify the matter further by not proposing a terminology grouping under one name all cases of anomalies due to acceleration, under another one all those due to retardation. Furthermore, GOULD (1977 : 229) recognized four categories of phenotypic anomalies due to *heterochrony* according to *whether* somatic features *or* reproductive organs have their development accelerated or retarded; this leaves apart the cases where *both* are accelerated or retarded in a same animal (*homochronic aneuchrony*).

7. Three kinds of criteria may be used for fixing the meaning of terms already used in the scientific literature: correct etymological meaning; first meaning given to the term by the author who coined it; use and tradition. All three kinds of criteria have their strong supporters, but I think that no general rule is valid and that one or another may be used

according to the situation. In the proposals made here, some terms are used in their original sense, others in their etymological sense, others in their usual sense.

In a field like this one, where already so many words have been coined (see GOULD, 1977: 432, note 3), it may seem foolish to try and introduce still new terms. However, and much as I dislike to do so, I have not seen any other solution, to designate some new categories, than create new names.

Also an important point is the following: I agree with GOULD (1977) that the study of *heterochrony* (or of *aneuchrony*) will be of a great importance in the evolutionary biology of tomorrow. Non-specialists (like myself) will have to introduce themselves into this field, and they will certainly appreciate the existence of a very clear, simple and "self-speaking" terminology. By "self-speaking", I have in mind a terminology where categories standing in some relation (opposition, or subordination) one to the other are indicated as such by the presence of a common root. This principle has been the most important one used for the choice of the terms that I shall now explain.

The use of the terms *total* and *partial* with respect to *neoteny* has been discussed elsewhere (DUBOIS, 1979). All phenomenons related to *aneuchrony* may be dealt with following a double "crossed" dichotomy: that between *total* and *partial* (which is general), and that between *definitive* and *temporary* (which applies only to phenomenons related to retardation). This point will not be discussed further here.

PROPOSALS FOR A TERMINOLOGY

1. Classification of anomalies in terms of results

a. *Paedomorphism.*

I shall now discuss the choice of categories and terms for a purely *descriptive* classification of anomalies due to *aneuchrony*, irrespective of the processes involved in their appearance.

First of all, I think we need a general, collective term for all phenotypes resulting from a phenomenon of *aneuchrony* and in which ancestral juvenile characters are present in the adult stage of a descendant, should those "juvenile characters" belong to the category of "somatic features" or to that of "reproductive organs", and whatever the processes involved in the origin of such variations. I cannot find a single existing word for this purpose, and I am therefore led to coin a new term. I suggest the term *paedomorphism* (*pais*: child; *morphe*: shape), which means "aspect of a child" and may therefore refer to the existence of juvenile characters in an adult animal.

Paedomorphism may affect both "somatic features" and "reproductive organs", or only part of them. *Total paedomorphism* is obtained when the whole phenotype of the animal remains juvenile: in this case, the process responsible for *paedomorphism* is clearly retardation. *Total paedomorphism* may be *definitive* ("definitive juveniles", which remain unable to reproduce) or *temporary* (development is only delayed, but finally occurs); both these cases may arise in nature, but they have also been obtained in artificial conditions in the laboratory.

All other cases of *paedomorphism* belong to the category of *partial paedomorphism*. In such cases, *heterochrony* is involved, leading to composite phenotypes, i.e. animals having, compared to their "normal" relatives, some "adult" and some "juvenile" characters. The

characters which are "juvenile" may remain so for the whole life (*definitive partial paedomorphism*) or become "adult" after some delay (*temporary partial paedomorphism*). Both acceleration and retardation of development may be responsible for the occurrence of *partial paedomorphism.*

The word *paedomorphism* is based on the same roots as the word *paedomorphosis* but is proposed instead of this later word in order to make it clear that it applies to a different category. In the use of GOULD (1977), *paedomorphosis* refers to some only of the cases of *paedomorphism*, those where adult reproductive organs are found in animals having on the whole a juvenile phenotype, but excludes the other cases.

b. *Partial paedomorphism and paedogenesis.*

The different possible combinations of "adult" and "juvenile" characters observed in given individuals are very numerous, and it does not seem necessary to create names for every one of them: such names would artificially subdivide a continuum of anomalies of a same kind. At one end of this continuum stand animals having only one feature "juvenile" in an overall "adult" phenotype: this is for example the case of an adult *Bufo bufo* which had retained its tail (OLIVIER, 1893), or other similar anomalies (DUBOIS, 1979; BREUIL, 1981); this is also the case of animals which are phenotypically adult but whose gonads are not adult (sexual maturation delayed or even suppressed). At the other end of the continuum stand animals having most features "juvenile" and only a few "adult" characters, like those Urodela which exhibit an overall larval phenotype but are sexually mature. Between these two extreme cases various combinations of "adult" and "juvenile" characters are to be found: thus in the Urodela which are able to breed although they have a "larval" phenotype, in some cases most of the somatic phenotype is "larval", while in others only a few somatic features are so (NOBLE, 1931).

Although the distinction is, for the reasons stated above, largely artificial, it seems useful to have a term for calling those cases of *partial paedomorphism* where the "reproductive organs" are in the adult condition, while all, or an important part, of the "somatic features" are in a pre-adult condition. Specifying "an important part" of the overall phenotype is meant to exclude from this category those cases, such as the tailed adult *Bufo*, where only one feature or a few features are concerned; but this clearly points to the artificial nature of the category.

A name is needed for this category. GOULD (1977) used the term *paedomorphosis* for this purpose, but, as discussed above, it seems better to retain this term, in the substitute form *paedomorphism*, for a more general category. PIERCE & SMITH (1979) suggested the use of the term *neoteny sensu lato* for this category. However, the term *neoteny* is also used by them to describe anomalies in terms of processes (*neoteny sensu stricto*). The use of a single term in both a purely descriptive and an explanative sense should be avoided, since it is liable to create confusions. The use of the word *neoteny* proposed below still leaves this term have both a "wide" and a "narrow" sense, but these are not those advocated by PIERCE & SMITH (1979).

Rather than coin a new term, I propose to use for the category defined above the term *paedogenesis*. I am aware that doing so I propose an even new use for a term which has already been used in different senses, but my reasons are as follows: (1) This use is consistent with the etymological meaning of the word (*pais*: child; *genesis*: generation): it means that an animal having a totally or largely juvenile phenotype is able to

reproduce. (2) For the phenomenon for which the term was created by VON BAER (1866), namely a special type of parthenogenesis, taking place in the gonads of still larval animals, I have previously (DUBOIS, 1979) proposed the term *parthenopaedogenesis*, which is etymologically clearer and avoids confusions. (3) Indeed, it is a long time since *paedogenesis* has lost its original meaning, except in entomological works dealing with a few particular cases (GOULD, 1977). The name *paedogenesis* has been used to designate both the process of "precocious sexual maturation of an organism still in a morphologically juvenile stage" (GOULD, 1977: 484) and the mere phenotypic result of "larvae able to reproduce", irrespective of the processes involved in this phenomenon (DENT, 1968). I here advocate the use of the word in this latest sense, because, the word having lost its original sense and no consensus having been reached until now as to the sense of the word, the etymology should in my opinion play the major role in trying to "fix" the sense of the term. (4) Both words *paedomorphism* and *paedogenesis* are based on the same root *paedo-*, which illustrates the fact that they are related concepts. In fact, *paedogenesis* is only a particular case of *paedomorphism*: its delimitation from other cases of *paedomorphism* is furthermore partly artificial.

2. Classification of anomalies in terms of processes

As submitted by GOULD (1977), all cases of *heterochrony* (and of *aneuchrony*) may be reduced to two types of processes: *acceleration* and *retardation*. It seems therefore useful to dispose of two different terms to designate anomalies due to both kinds of processes.

Within these anomalies, it may also be useful to distinguish as a special category those which result in "reproduction in a non-adult phenotype", i.e., according to the present terminology, cases of *paedogenesis*.

a. *Neoteny.*

The word *neoteny* (*neos*: young; *teino*: I lengthen) refers etymologically to the prolongation of the juvenile state, and could therefore be used, in a wide sense, to designate all anomalies due to *retardation* of development. Retardation may either bear on the whole phenotype (*total neoteny s.l.*), or on certain characters only (*partial neoteny s.l.*).

This use of *neoteny* is wider than the usual one, and especially than that advocated by GOULD (1977), who restricts the use of the term to anomalies due to retardation of somatic development. This later type of anomalies is designated by PIERCE & SMITH (1979) as *neoteny sensu stricto*. I propose to retain this later suggestion. *Neoteny sensu stricto* is but a special type of *partial neoteny sensu lato*, where only the somatic features (or most of them) have their development retarded, while the reproductive organs follow a normal development; as far as the phenotype alone is concerned, this is a kind of *paedogenesis*, *paedogenesis* due to retardation.

b. *Neosystelly.*

No word is presently available to designate all anomalies and variations due to an *acceleration* of development, and I find myself again obliged to coin a new term. Since this category stands opposed to the category of *neoteny (s.l.)*, I suggest to use the same root *neo-* for the new word. I therefore propose the term *neosystelly (neos*: young; *systello*: I shorten) for this type of anomalies. If all somatic features and the reproductive organs show an acceleration in their development (*total neosystelly*), adulthood will be more pre-

Table I. — Categories of anomalies due to aneuchrony.
In black : categories of anomalies in terms of results.
In italics : categories of anomalies in terms of processes

Types of organs affected	Type of aneuchrony	
	Acceleration *(neosystelly)*	Retardation *(neoteny s.l.)* [1]
All somatic features + reproductive organs	**Precocious Adulthood** *total neosystelly*	**Total Paedomorphism** *total neoteny s.l.*
Reproductive organs alone	**Paedogenesis** *partial neosystelly (progenesis)*	**Partial Paedomorphism** *partial neoteny s.l.*
All or most of somatic features	**Partial Paedomorphism** *partial neosystelly*	**Paedogenesis** *partial neoteny s.l. (neoteny s.str.)*
Just a few somatic features (even a single one)	**Partial Paedomorphism** *partial neosystelly*	**Partil Paedomorphism** *partial neoteny s.l.*

1. All categories of *neoteny s.l.* (anomalies due to retardation) may be subdivided into *definitive* and *temporary*

cocious than usual; this is a special case of *aneuchrony* which does not lead to *paedomorphism.* In the other cases (*partial neosystelly*), only a part of the phenotype is subject to acceleration in development.

Finally, a special term may be searched for to designate the cases of *partial neosystelly* consisting in an acceleration of the development of reproductive organs alone, which leads to a *paedogenetic* phenotype. For this category, the word *progenesis*, used in the same sense as in GOULD (1977), is available.

To sum up, if processes are taken into account, all cases of *paedomorphism* fall into two categories (*neoteny s.l.* and *neosystelly*), as do all cases of *paedogenesis* (a particular case of *paedomorphism*), which may belong to either *neoteny s. str.* or *progenesis.*

The relations of the various terms proposed here between themselves are shown in Table I, while Table II gives definitions of the terms and correspondence between the terminology suggested and those of GOULD (1977) and of PIERCE & SMITH (1979).

RÉSUMÉ

Une nouvelle terminologie est proposée pour tous les cas de variations ou d'anomalies dus à des phénomènes d'*aneuchronie* (accélération ou ralentissement du développement lors de l'ontogénie). Ces anomalies peuvent être simplement décrites en termes de résultats morphologiques : les mots choisis pour les désigner *(pédomorphisme, pédogenèse)* ont en commun le préfixe *pédo-*. Les mêmes anomalies peuvent être classées en fonction du type de processus développementaux impliqué dans leur genèse : s'il s'agit de *ralentissement,* les anomalies appartiennent à la catégorie de la *néoténie s.l.,* et s'il s'agit d'*accélération,* à celle de la *néosystellie ;* les deux termes commencent par le préfixe *néo-*. Enfin, les termes *néoténie s. str.* et *progenèse* sont choisis pour désigner les deux types distincts de *pédogenèse,* dus respectivement au ralentissement et à l'accélération du développement.

Table II. — Definition of terms and correspondence between the terminology suggested here and those of GOULD (1977) and of PIERCE & SMITH (1979).

Suggested terminology	Definition	GOULD's (1977) terminology	PIERCE & SMITH's (1979) terminology
Paedomorphism	Presence of juvenile features in the adult stage	(no name)	(no name)
Paedogenesis	Reproductive organs in the adult condition, while most or all of the somatic features are in a juvenile condition	paedomorphosis	neoteny s.l.
Neoteny s.l.	Paedomorphism due to retardation in development	(no name)	(no name)
Neoteny s. str.	Paedogenesis due to retardation in the development of somatic features	neoteny	neoteny s.str.
Neosystelly	All phenotypic anomalies due to acceleration in development	(no name)	(no name)
Progenesis	Paedogenesis due to acceleration in the development of reproductive organs	progenesis	paedogenesis

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